

A STUDY OF MALE GENITALIA IN BRUCHIDAE (COLEOPTERA)

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ABSTRACT—Nomenclature is given for various parts of the male genital apparatus, and illustrations showing a number of variations are provided. A section on the musculature of male genitalia and a table giving correlative terms used by other workers is included.

Descriptions of genera and most species in the Bruchidae have until recently stressed characteristics of color and pattern, sculpture of the dorsum of the body, antennal form, and size and number of teeth on the ventral margin of the hind femur. Inadequate descriptions and infrequent illustrations have led to much confusion in the classification of this family.

Male genitalia have been adequately illustrated for only a few species of Bruchidae, and less than ten generic treatments have utilized the specific characters in these organs. Hoffmann (1945) illustrated the genitalia for nearly all of the Bruchidae of France, but his figures are of only the external profiles of the male organs with no internal structures shown. Dissections of male genitalia of about 900 specimens of about 400 species of Bruchidae from all over the world disclosed a rich source of consistent and apparently reliable characteristics for specific identification, and, in some cases, generic and subgeneric definition.

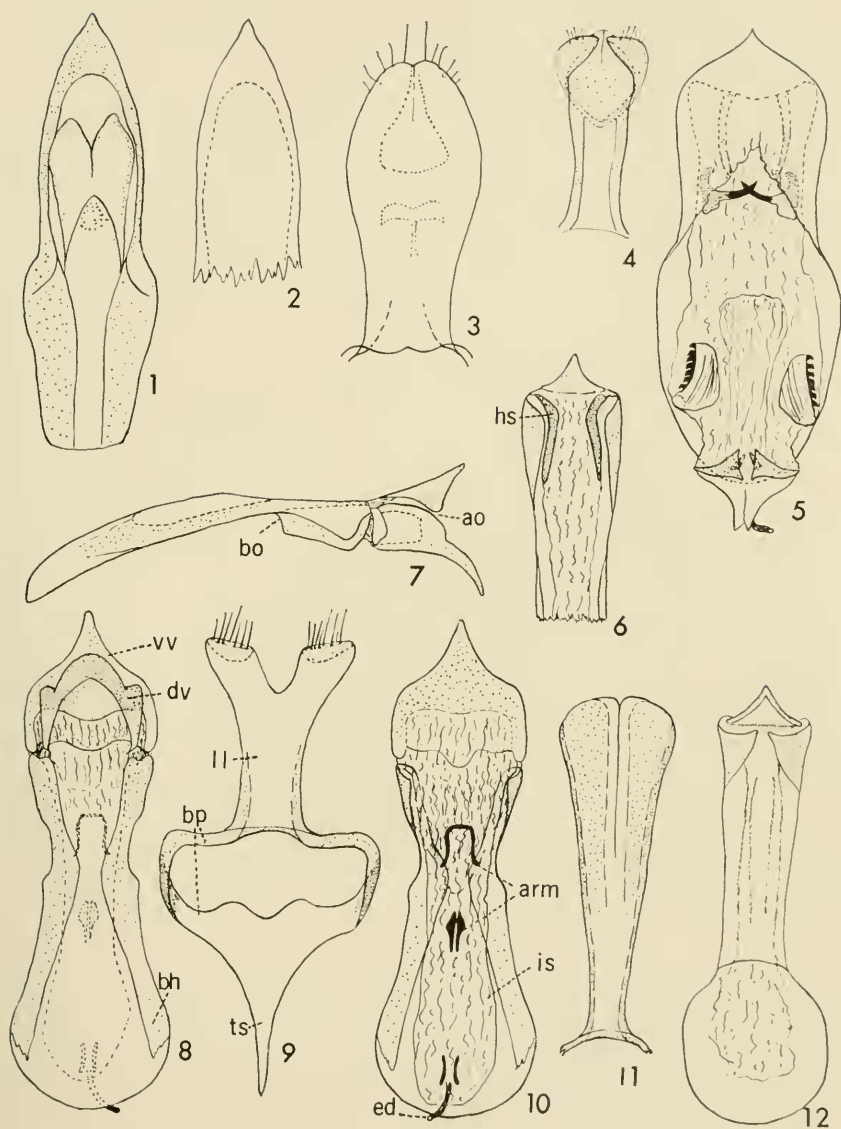
The present paper proposes a nomenclature for male genitalia of the Bruchidae, presents illustrations and short descriptions of 12 diverse species, and outlines the basic musculature of the male organs. I hope that this presentation will help stimulate investigations using genitalia in classification of this family, and will help stabilize nomenclature used in the descriptions.²

TECHNIQUES AND PROCEDURES

Satisfactory results in the use of male genitalia of Bruchidae for identification require consistent and careful technique of preparation

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² After this manuscript was accepted by the editor, I received a reprint of a paper by Dr. A. Teran, Tucuman, Argentina, entitled "Observaciones sobre las Estructuras Genitales de los Machos de Diversos Generos de Bruchidae (Coleoptera)" published in *Acta Zoologica Lilloana* 22, p. 307-336. Included are discussions and illustrations of genitalia of the following species: *Algarobius prosopis* (Le Conte), *Amblycerus* prob. *hoffmanseggi* (Gyllenhal), *Caryedes brasiliensis* (Thunberg), *Kytorhinus prolixus* (Fall), *Megacerus discoidus* (Say), *Meibomeus musculus* (Say), *Neltumius arizonensis* (Schaeffer), *Rhaebus solskyi* Kraatz, *Zabrotes subfasciatus* (Boheman) and *Megacerus coryphae* (Olivier).



Figs. 1-3, *Caryoborus priocerus* (Chev.): 1, median lobe, dorsal; 2, median lobe, ventral; 3, lateral lobes, dorsal. Figs. 4 & 5, *C. glediata* (L.): 4, lateral lobes, dorsal; 5, median lobe, ventral. Fig. 6, *Caryedes albotectus* (Sharp): median lobe, ventral of apex. Figs. 7-10, *Amblycerus robiniae* (F.): 7, median lobe, lateral; 8, median lobe, dorsal; 9, tegmen; 10, median lobe, ventral. Figs. 11 & 12, *Acanthoscelides obtectus* (Say): 11, lateral lobes, dorsal; 12, median lobe, ventral.

of the parts for examination and comparison. In order to see the various sclerotized parts of the internal sac and to properly observe the configuration of the median lobe and lateral lobes, I have used the following procedure successfully.

The completely relaxed beetle is held with the pygidium uppermost between thumb and forefinger under the dissecting microscope. With fine forceps, the apex of the pygidium is gently lifted to expose the genitalia. A drop of alcohol is then placed in the opening to soften the tissues, the supporting membranes are severed with a fine needle, and the entire mass is removed with the forceps. The pygidium is then carefully restored to its normal closed state. Removal of the entire abdomen from very small specimens may be necessary to prevent extensive damage to the specimen.

The visceral mass containing the genitalia is then placed into a cold, 10% KOH solution for 12 to 16 hours to remove muscle fibers and fat, or into a 150° F. solution for not more than ten minutes. Excessive clearing will break down the resilience of the sclerotized parts, but insufficient clearing will fail to remove the tissues. Cleared genitalia should be washed in distilled water to remove the KOH and float away the tissues, then washed in 70% alcohol to remove trapped air, and finally removed to glycerin for observation.

For temporary storage during the study and comparison phases, I use plastic vial caps (Kingsolver, 1962) containing glycerin. If these storage containers are properly labeled, any number of preparations may be kept ready for immediate use in comparisons. Permanent storage is in microvials the stoppers of which are impaled on the pin for positive association (Gurney *et al.*, 1964).

For purposes of drawing, genital parts are placed in glycerin in a deep well slide or concave slide and held in place by *minuten nadeln* or glycerin gel. To obtain the proper proportions in the drawing, either a camera lucida, a microprojector, or squared ocular grid is used.

NOMENCLATURE

The morphological terms used by Snodgrass (1935, 1957) have never been generally accepted by coleopterists because of the strong influence of the terminology used by Sharp and Muir (1912) in their classical study of male terminalia of Coleoptera. The nomenclature that I have adopted for this and future papers on Bruchidae is largely that of Sharp and Muir with some modification of terms because of certain peculiarities found in this family. A list of these terms with the equivalent used by Snodgrass and others is given at the end of the morphological discussion. Mukerji and Chatterjee (1951) have followed Snodgrass in terminology as have Southgate, Howe, and Brett (1957, 1958) in their papers, and Hieke (1966) in his recent impor-

tant contribution to the morphology and musculature of male genitalia of Coleoptera.

GENERAL MORPHOLOGY

The male genitalia of Bruchidae are modified from the cucujoid type and are basically similar to those found in Cerambycidae, Chrysomelidae, and Curculionoidea (the Phytophaga).

The genital complex is composed of three principal parts—the *tegmen* with its *lateral lobes* and *tegmina* (fig. 9), the *median lobe* (figs. 7, 8, 10), and the *internal sac* with its associated sclerotized structures (fig. 10). The associated musculature is discussed in a separate section.

In the Bruchidae, the *lateral lobes*, the *basal piece*, and the *tegmina* are fused into one structure, the *tegmen*, which serves as a muscle and membrane attachment and as a guiding mechanism for the median lobe. As in other Phytophaga, the lateral lobes lie primitively on the dorsal side of the median lobe with their apices just above the median orifice and their bases attached to the ring-like basal piece. The lateral lobes are usually separated by a deep cleft, but in certain primitive groups they are fused into a strap-like structure simply expanded at the apex, or into a sheath-like structure surrounding the median lobe. Sensitive setae usually fringe the apical margins of the lateral lobes.

The *basal piece* surrounds the median portion of the median lobe and with the *tegmina* forms important attachments for muscles of the median lobe. The *tegmina* is often alate vertically or horizontally to provide more surface for muscle anchoring. Its function is discussed with that of the median lobe.

The median lobe varies in details of form throughout the family, but is essentially a sclerotized tube carrying the *internal sac* and its retractor muscles and the ejaculatory duct. The internal sac is attached near the apex of the median lobe at the apical orifice. In some primitive genera of Bruchidae (e.g., *Caryopemon*, *Caryobruchus*, *Pachymerus*) the median lobe is very similar to the one-piece tubular type found in the Cerambycidae and Chrysomelidae, but in nearly all other Bruchidae that I have examined, the apex of the median lobe bears one or more valve-like sclerites guarding the apical orifice. These sclerites articulate with the main body of the median lobe by membranous connections or thinly sclerotized, partly fractured bands. In certain genera (e.g., *Amblycerus*) both *dorsal* and *ventral* valves are present, but in the majority of the Bruchidae (e.g., Kytorhininae, most Bruchinae, Eubaptinae, some Amblycerinae) the dorsal valve is lacking. In its place there is often a membranous hood-like structure overhanging the apical orifice. Powell (1941) illustrates for several species

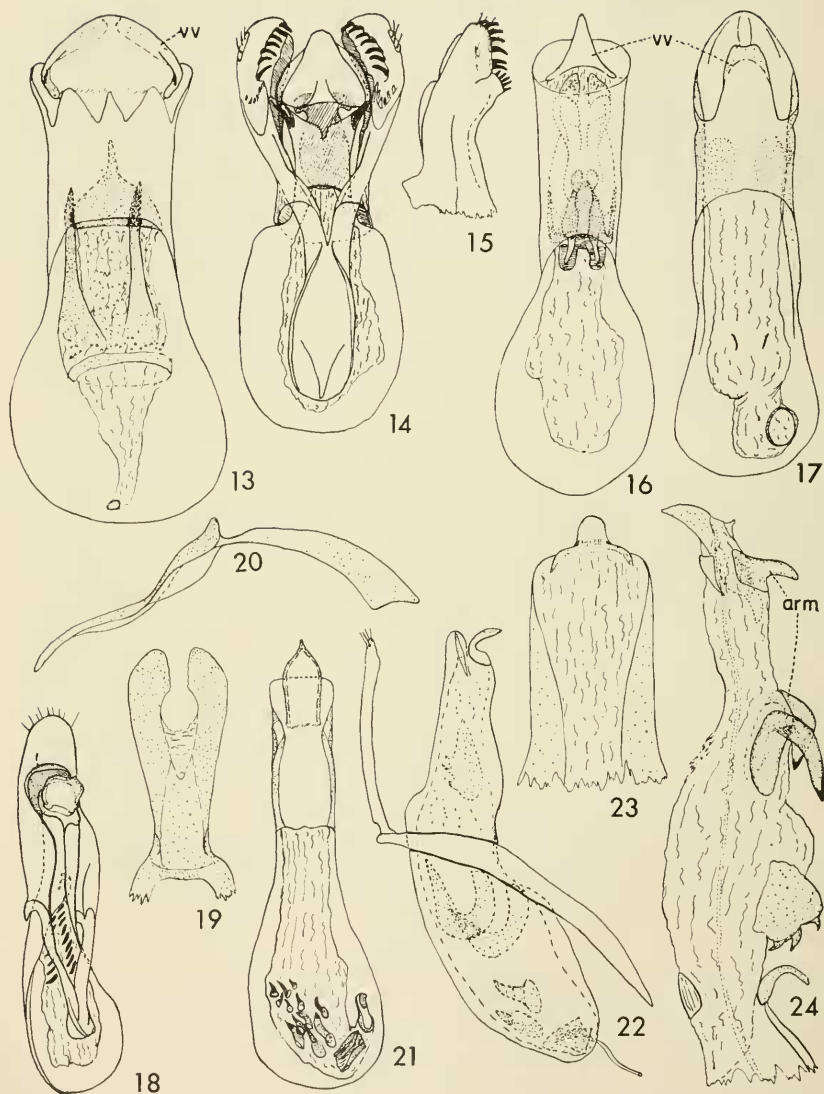


Fig. 13, *Merobruchus julianus* (Horn.): median lobe, ventral. Figs. 14 & 15, *Bruchidius modicus* (Lea): 14, median lobe & tegmen, ventral; 15, right lateral lobe, lateral. Fig. 16, *Kytorhinus* sp.: median lobe, ventral. Fig. 17, *Mimosestes sallaei* (Sharp): median lobe, ventral. Fig. 18, *Megacerus alternatus* Brid.: median lobe & tegmen, ventro-lateral. Figs. 19–21, *Althaeus hibisci* (Oliv.): 19, lateral lobes, dorsal; 20, lateral lobes, lateral; 21, median lobe, ventral. Figs. 22–24, *Pseudopachymerina spinipes* (Eric.): 22, median lobe & tegmen, lateral; 23, median lobe, ventral of apex; 24, everted internal sac, lateral.

of Chrysomelidae an "apical hood" which is probably homologous with the structure I am terming "dorsal valve." The distinctive ventral valve in the Bruchidae seems to be a unique development, at least among the Phytophaga. The ventral valve is probably the structure termed "exophallic valve" by Mukerji and Chatterjee (1951), but they worked with species having only the ventral valve and offered no term for the corresponding dorsal valve. The role of the ventral valve in copulation is not well understood but in conjunction with the lateral lobes it appears to be a sensory organ to aid in positioning the apical orifice opposite the opening of the female genital tract. Probable transition steps in the isolation of the ventral valve from the remainder of the median lobe may be illustrated by comparing in turn figures 1, 5, 10, 13, 12. In the genus *Mimosestes* (fig. 17), the ventral valve has either degenerated or has lost its articulation with the main body of the median lobe, or the tongue-like lobe never developed articulation. In the genus *Caryedes* (fig. 6), a secondary articulation has developed in the body of the elongated median lobe in addition to the ventral valve.

In a number of species in several genera, there is on either side of the apical orifice an additional pair of curved lateral sclerites to which I here give the name "hinge sclerites" (fig. 6, hs). These are imbedded in the wall of the internal sac and may impart a springlike action to aid in eversion of the sac, or may simply assist in positioning the apical orifice during the first stages of copulation. Near the base of the median lobe is the basal orifice which is penetrated in most species by the apex of the internal sac in repose, and through which the *ejaculatory duct* and the *retractor muscles* are threaded during eversion of the sac.

In many Coleoptera, the base of the median lobe is prolonged anteriorly into a pair of straplike apodemes, the *basal struts* or *aedeagal apodemes*. These serve as attachment points for the muscles which move the median lobe within the tegmen, and for the retractor muscles of the internal sac. In most Bruchidae, as in many Chrysomelidae (Powell, 1941 and Iablokoff-Khnzorian, 1966), these struts are greatly expanded laterally into a *basal hood*, or *cucullus*. Fitting into the ventral cavity of the hood is the expanded *tegmenal strut* of the tegmen. Thick muscle bands connecting the rim of the hood with the tegmenal strut completely enclose the ventral opening of the basal hood, the entire structure forming an auxiliary pump (the phallic bulb of Mukerji and Bhuya, 1937) to evert and distend the internal sac, and in effect fuse the median lobe and tegmen into one functional unit at the same time. This structure and its function was first described for Bruchidae by Mukerji and Bhuya (1937).

The medium of inflation is undoubtedly haemolymph siphoned through the relaxed muscle fibers between compressions of the pump, but prevented from escaping by the expanded fibers during compres-

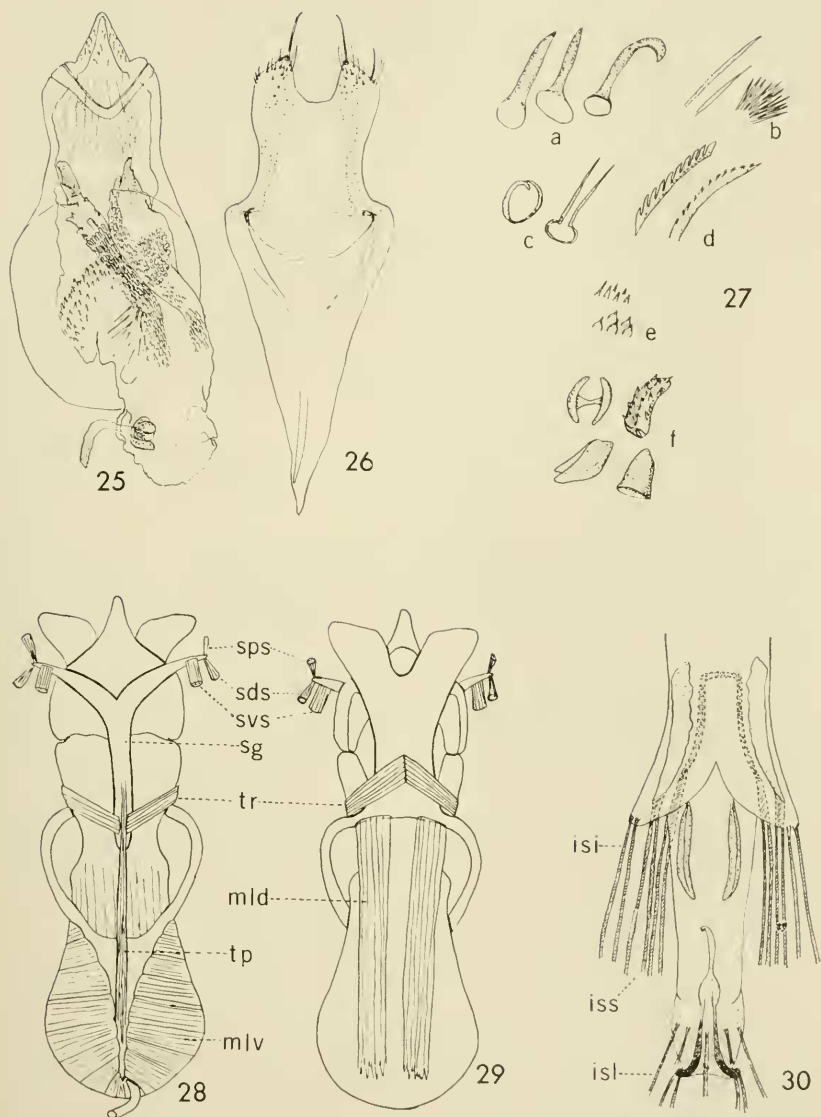
sion. Retraction of the internal sac is effected by the retractor muscles with origins on the dorsal internal surface of the basal hood, and insertions on the internal sac wall at the gonopore sclerites, at about the middle of the sac usually on one or more of the armature sclerites, and near the base of the sac. Using the genitalia of a freshly killed specimen of *Algarobius prosopis* (LeConte), I was able to partly duplicate the process of eversion of the internal sac by pumping the base of the median lobe with fine forceps, complete eversion apparently being prevented by the tension of the retractor muscles.

The internal sac, in the few species observed (with one known exception), is the only part of the male genitalia to actually penetrate the vaginal duct. The apex of the median lobe and the lateral lobes apparently serve as guides to position the median lobe opposite the vaginal opening. The one observed exception is in *Mimosestes sallaei* (Sharp) in which the median lobe and the lateral lobes together enter the vaginal tract. It may be significant that in this genus, the ventral valve is fused and rigid, formed as an extension of the ventral wall of the median lobe rather than as a moveable valve.

The external surface of the everted internal sac in Bruchidae is usually armed with variously shaped sclerites (e.g., denticles, hooks, spines) which apparently serve as holding devices during copulation. Arrangement and shape of the armature is usually characteristic for each of the species. The armature of the retracted internal sac is visible through the walls of the median lobe in cleared preparations but exact spatial relationships of the armature sclerites is often difficult to determine in this position. Successful eversion by using tools made of hooked *minuten nadeln* is usually possible only in the larger species. Until a suitable technique is devised for consistently everting the internal sac of smaller species, only the shape of individual armatural sclerites can be used as taxonomic characters, but these are apparently diagnostic as is indicated by numerous series of specimens which have been cleared and studied.

The form, arrangement, and number of the sclerotized ornamentations of the wall of the internal sac in many instances provide the basis for species definition in the Bruchidae. A definition of terms applicable to this armature is necessary for precise descriptions. With lack of comparative material, detailed illustrations of the male genital parts are necessary for identification of many species; however, drawings of the armature in flat plate illustration cannot always demonstrate critical three-dimensional characteristics.

The armature which anchors the internal sac in place during copulation is an outgrowth of the sac; however, while the sac is in repose this armature projects into the pseudolumen formed by the sac. The internal sac is in reality an extension of the median lobe (whether or



Figs. 25 & 26, *Eubaptus palliatus* Lac.: 25, median lobe, ventral; 26, tegmen, dorsal. Fig. 27, various types of armature of the internal sac in the Bruchidae. Figs. 28-30, *Amblycerus robiniae* (F.): 28, musculature of median lobe, tegmen and spiculum gastrale, ventral; 29, same, dorsal; 30, diagrammatic sketch of principal muscle bands of internal sac.

not it can be everted for study) but to avoid confusion of terms, the terminology of orientation applied to the sac should be that of the everted state even though sclerites surrounding the apically located gonopore appear to lie near the base of the median lobe proper in repose. Thus, the gonopore must be regarded as apical in respect to the sac regardless of the everted or retracted state of the sac, and the basal region of the sac must be that nearest the apical orifice of the median lobe.

No overall basic pattern in the arrangement of the armature has been discovered so far although closely related species usually have somewhat similar basic patterns. Descriptions of location of the various sclerites are necessarily independent. Variations in the form and size of the individual sclerites is nearly infinite. Certain basic types can be classified although descriptive terms applied to the armature types are of necessity somewhat arbitrary. The major types observed are as follows:

Spines—Fig. 27a. Of various sizes but always with expanded base (as in a rose thorn). May be straight, curved or recurved, in pairs or single. Also see figs. 5, 13, 21, 22, 24.

Spicules—Fig. 27b. Long, slender, needle-like without expanded base. Often appears in echinous clusters.

Denticles—Fig. 27e. Short, flat, broad at base, acute apically. Often set in rows on main body of internal sac where they may be termed "teeth."

Gonopore sclerites—Fig. 27c. Various shaped, often intricate, and usually bilaterally symmetrical. Probably part of the mechanism forming the spermatophore. Also see figs. 5, 16, 24.

Serrata—Fig. 27d. Blade-like with row or rows of teeth on one or both edges.

Irregulars—Fig. 27f. Amorphous, asymmetrical, birescentic, ovoid, or reniform. May be armed with denticles on external surface. Also see figs. 5, 24, 25.

Various combinations and intergrades can be found.

MUSCLES OF THE MALE GENITALIA IN BRUCHIDAE

Other studies of musculature of the male genitalia of Coleoptera were consulted and an attempt was made to correlate those found in Bruchidae. The most useful of these studies were by Evans (1961), Pu (1938), Hieke (1966), Bissel (1937), and Muir (1919). The best correlations were possible with studies in Coleoptera Phytophaga although differences in insertion were noted and certain muscles are lacking in Bruchidae because of a shift in functional emphasis. Evans' paper (1961) on *Atomaria* (Cryptophagidae) is very well done, but the inversion of position of lateral lobes in relation to the median lobe

TABLE OF HOMOLOGIES

Present Paper	Sharp & Muir	Snodgrass	Mukerji et al.
median lobe	median lobe	aedeagus	aedeagus
tegmen	tegmen	_____	_____
basal piece	basal piece	phallobase	tegmen
tegmenal strut	tegmenal strut	_____	tegmenal strut
lateral lobes	lateral lobes	parameres	parameres
apical orifice	median orifice	phallotreme	median orifice
basal orifice	_____	_____	_____
basal hood	median strut	aedeagal apodeme	dorsal plate
internal sac	internal sac	endophallus	phallosome
hinge sclerites	_____	_____	_____
dorsal valve	_____	_____	_____
ventral valve	_____	_____	end plate & exophallic valve

in this family compared with that in the Phytophaga left some doubt in actual correlation. Hieke's paper on musculature of genitalia of three species of Coleoptera is one of the most meticulous and complete studies I have seen; however, he uses the Snodgrass terminology for parts of the genitalic complex, and as I have noted earlier in this paper, I favor the use of Sharp and Muir's terminology because of its wider acceptance by coleopterists. Evans uses the latter terminology, and I have tried to follow her designations of muscle groups as closely as possible. Not all of the muscle groups in the seventh and eighth somites have been identified in the present paper, but the principal bands concerned with protrusion and retraction of the median lobe, internal sac, tegmen, and spiculum gastrale are included. Muscles associated with the rectum are not included here. Wherever I was able to definitely correlate bundles of muscles in Bruchidae with those in either *Atomaria* (Evans, 1961), or *Strangalia* (Muir, 1919), I have inserted their designations after the description of the muscle.

CLASSIFICATION OF MUSCLE BANDS

- I. Suspensor muscles of the spiculum gastrale (figs. 28, 29).
 - a. Dorsal suspensor muscle—origin on eighth tergite, insertion on lateral arm of spiculum gastrale.
 - b. Posterior suspensor muscle—origin on eighth tergite, insertion on lateral arm.
 - c. Ventral suspensor muscle—origin on eighth sternite, insertion on lateral arm.

II. Muscles moving tegmen in relation to spiculum gastrale (figs. 28, 29).

- a. Protractor muscle—origin on anterior end of spiculum and insertion on ventral ridge of tegminal strut. Moves tegmen (and median lobe) posteriorly in body. (Evans-TEPA, Muir-g).
- b. Retractor muscle—origin on lateral margins at anterior end of spiculum, extends dorsad around median lobe and inserts on lateral margins of base of lateral lobes or on second connecting membrane above lateral margins of lateral lobes posterior to the tegmen ring. The function is to retract the tegmen and median lobe. This muscle band undoubtedly is homologous with TED of Evans which she regarded as a depressor of the tegmen. Since the tegmen and the median lobe are bound together in the Bruchidae, this band also serves as a retractor for the combined units. I could find no muscles in Bruchidae corresponding to the posterior protrusor and retractor muscles of the tegmen found in *Ato-maria* by Evans.

III. Muscles moving tegmen in relation to median lobe (figs. 28, 29).

- a. Dorsal muscles of median lobe (MLD). Origin on anterior dorsal margin of tegmen and insertion on dorsal surface of basal hood along dorsal apodemes. The function is to elevate the lateral lobes during copulation. Another probable function is that of antagonist of the MLV muscles (see below) during the pumping action of the basal bulb. These bands are probably composed of a portion of the protrusor muscles of median lobe (Evans, PEP), but the function has been modified because of the integration of the two sets of lobes.
- b. Ventral muscles (MLV). (Compressor muscles—Mukerji and Bhuya). Origin on lateral margins of tegminal strut and tegmen ring and insertion on latero-ventral margins of basal hood. This large muscle mass completely encloses the ventral opening of the basal hood and forms a basal bulb-like structure (phallic bulb, Mukerji and Bhuya, 1937) whose purpose is to evert the internal sac during copulation. The pump formed in this way is not unique in Bruchidae, but is more highly developed in this family than in observed Cerambycidae or Chrysomelidae. The presence of a basal pump is probably more prevalent in the Phytophaga than is generally realized. Because of the great development of these muscles in Bruchidae, the median lobe and the tegmen are strongly bound together and function as a unit in

movement in and out of the body. The common ejaculatory duct is threaded between the muscle bands at the anterior end of the median lobe to join the internal sac which is completely enclosed inside the basal pump. The ventral muscles are difficult to homologize individually with Evans' or Muir's examples in *Atomaria* and *Strangalia* respectively, but appear more likely to be a recombination of those muscle bands shifted in their origin, insertion, and function for a specific purpose. They are here interpreted as being composed of portions of the protrusor muscles of the median lobe (Evans-PEP, Muir-d), the compressor muscles of the internal sac (Evans-ISC, Muir-n), and the retractor muscle of the median lobe (Evans-PER, Muir-c). The latter muscle bands extending between the ventral margin of the median foramen and the posterior ventral margin of the tegmen ring (Evans-PER, Muir-c) have not been found in that precise position in any of the species of Bruchidae examined so far. In their place is a tough sclerotized connecting membrane which helps to seal the pressure inside the median lobe during compression of the basal bulb. It is another example of alteration due to a shift in function in the Bruchidae.

IV. Retractor muscles of the internal sac (fig. 30).

Origin on the ventral surface of the basal hood inside the basal pump and insertion in varying positions on the internal sac. The long muscles (ISL) are inserted on the internal sac usually on a pair of sclerites flanking the gonopore. During eversion of the sac in copulation, these muscles extend from their origin through the entire length of the median lobe and the internal sac. They undoubtedly are the first to contract during retraction of the internal sac following copulation.

The intermediate (ISI) and short (ISS) muscle bands insert at various points on the sac and retract the bulkier parts of the sac, i.e., the sclerites and lobes of the sac. Some of the larger spines in the internal sac of certain species probably require individual strands of muscle to disengage them from the interior of the female genital tract. Mukerji and Bhuya (1937) erroneously concluded that the retractor muscles originated on the tegminal strut.

DISCUSSION OF FUNCTION

The coincidental functional shifts in development of (1) a simple internal sac into a complex intromittent organ, (2) the development

of simple protractor muscles into strong, basal, pump compressor muscles to extrude the sac, (3) the fusion of the median lobe and the tegmen into one functional unit, (4) the fracturing of the ventral valve from the main body of the median lobe to presumably serve as a guide during copulation, (5) the transformation of muscle bands between the tegmen ring and the basal orifice into membrane are all significant basic changes undoubtedly reflecting more complex mating procedures over those of related or more generalized groups. The focal point about which these changes took place is probably the production of spermatophores. To achieve complete expulsion of the gelatinous sperm-filled sac, continuous and uninterrupted copulation is necessary, and the sum of developments outlined above appear to be directed toward this purpose. More studies in mating habits are needed to elucidate these speculations.

DESCRIPTIONS OF REPRESENTATIVE SPECIES

It would be impossible to illustrate all of the modifications in the male genitalia of Bruchidae in this short paper. I intend to show here only a few of the principal types as a guide to identification of the various parts, and this, I hope, can be extended to apply to other species of Bruchidae as well. Approximately 400 identified and unidentified species of Bruchidae have been dissected for this and other studies, and these should provide a sufficient cross-section of types in this family.

The following descriptions are intended to help orient the parts for each species. The drawings for only one species, *Amblycerus robiniae* (F.) are completely labeled but corresponding parts in other species should be readily identifiable.

1. *Caryoborus priocerus* (Chevrolat). North America. Figs. 1, 2 & 3. Similar in structure to primitive Chrysomelidae and Cerambycidae. Apex of median lobe rigid; dorsal valve homologue membranous, bilobed. Lateral lobes fused on midline; internal sac without distinct armature.

2. *Caryobruchus gleditsiae* (L.). North America. Figs. 4 & 5. Apex of median lobe rigid, broader than in *C. priocerus*; dorsal valve (not shown) thinly sclerotized. Lateral lobes fused, straplike at base. Armature of internal sac as in fig. 5.

3. *Caryedes albotectus* (Sharp). Central and South America. Fig. 6. Apex of median lobe with separate ventral valve; base of internal sac with hinge sclerites (hs). Median lobe secondarily fractured.

4. *Amblycerus robiniae* (F.). North America. Figs. 7, 8, 9, 10, 28, 29 & 30. Dorsal valve (dv) trilobed, lightly sclerotized; ventral valve (vv) consisting of apical one-fourth of median lobe separated from the remainder by a thinly sclerotized area; basal hood (bh) concave ven-

trally, with lateral straplike thickenings (corresponding to basal apodemes in other families); basal orifice (bo); and apical orifice (ao) as in fig. 7. Armature of internal sac (is) consisting of U-shaped rod and two pairs of narrow sclerites of which one pair is apparently associated with the ejaculatory duct (ed) orifice. Lateral lobes (ll) fused on midline, straplike, divided terminally into two angular lobes with patches of setae; common base of lateral lobes attached to ring-like basal piece (bp) which is prolonged antero-ventrally into tegmental strut (ts). This species represents the probable first step in the isolation of the ventral valve from the remainder of the median lobe.

5. *Acanthoscelides obtectus* (Say). Cosmopolitan. Figs. 11 & 12. Median lobe flattened but with basal hood hemispherical, median one-half nearly membranous, apex reinforced with lateral, curved, sclerotized plates; ventral valve broadly triangular. Lateral lobes straplike basally, spatulate apically. Internal sac armed with very fine denticles in indistinct longitudinal rows.

6. *Merobruchus julianus* (Horn). North America. Fig. 13. Median lobe somewhat flattened with basal hood hemispherical, apex slightly expanded; ventral valve broad and rounded. Armature of internal sac with a broad flattened sclerite, two long, aciculate spines and numerous short denticles. Lateral lobes not illustrated.

7. *Bruchidius modicus* (Lea). Australia. Figs. 14 & 15. Middle part of median lobe abruptly narrowed then gradually expanded posteriorly into a hood-like membranous lobe nearly covering the ventral valve; ventral valve cordiform. Internal sac armed with vasiform sclerite. Lateral lobes greatly expanded laterally into massive spinose lobes nearly enclosing median lobe.

8. *Kytorhinus* sp. Fig. 16. Apex of median lobe hood-like; ventral valve acutely triangular. Armature of internal sac a complex of paired tubelike lobes and spicules. Lateral lobes not illustrated.

9. *Mimosestes sallaci* (Sharp). North America. Fig. 17. Median lobe flattened; basal hood scarcely expanded; apex hood-like; ventral valve a tongue-like lobe fused at base with main body of median lobe. Internal sac armed with two vague patches of spicules and a pair of small spines near apex. Lateral lobes not illustrated.

10. *Megacerus alternatus* Bridwell. Hawaii and North America. Fig. 18. (Three-quarters ventral aspect of median lobe and lateral lobes). Median lobe expanded basally, narrowed apically; apex hood-like; ventral valve shield shaped. Armature of internal sac with two rows of dark spines. Lateral lobes fused into hoodlike structure nearly enveloping median lobe.

11. *Althaeus hibisci* (Olivier). North America. Fig. 19, 20 & 21. Basal hood gradually expanded; apex of median lobe truncate; ventral valve long, narrow, and acute apically. Internal sac armature with

several thornlike spines and a flattened irregular plate. Lateral lobes with apices curved and concave meso-ventrally.

12. *Pseudopachymerina spinipes* (Erichson). South America. Figs. 22, 23 & 24. Basal hood relatively large; apex of median lobe blunt and rounded; ventral valve rounded at apex, broad at base, strongly curved in lateral aspect. Internal sac armature with two large, thornlike spines and two platelike sclerites at apex, paired median recurved spines, a basal, irregular, serrate sclerite, and a dorsal flattened plate; internal sac shown in repose in Fig. 22, and inflated in Fig. 24. Lateral lobes narrow and flattened.

13. *Eubaptus palliatus* Lacordaire. South America. Figs. 25 & 26. Median lobe short, basal hood broad; ventral valve partially membranous. Internal sac with two irregular, denticulate, spine-like processes; membrane denticulate; gonopore sclerite U-shaped. Lateral lobes broad at base, broadly emarginate and angularly lobed at apex.

ABBREVIATIONS USED IN ILLUSTRATIONS

- ao—apical orifice
- arm—armature of internal sac
- bo—basal orifice
- bp—basal piece
- bh—basal hood
- dv—dorsal valve
- ed—ejaculatory duct
- hs—hinge sclerite
- is—internal sac
- isi—intermediate muscles of internal sac
- isl—long muscles of internal sac
- iss—short muscles of internal sac
- ll—lateral lobe
- med—dorsal muscles of median lobe
- mlv—ventral muscles of median lobe
- sds—dorsal suspensor muscle of spiculum gastrale
- sg—spiculum gastrale
- sps—posterior suspensor muscle of spiculum gastrale
- svs—ventral suspensor muscle of spiculum gastrale
- tp—protractor muscle of tegmen
- tr—retractor muscle of tegmen
- ts—tegmenal strut
- vv—ventral valve

REFERENCES

- Bissell, T. H. 1937. Structure of the reproductive system of the pecan weevil (Curculionidae). *Ann. Ent. Soc. Amer.* 30(2):242-248.
- Cerezke, H. F. 1964. The morphology and functions of the reproductive systems of *Dendroctonus monticolae* Hopk. (Coleoptera: Scolytidae). *Can. Ent.* 96(3):477-500.

- Crowson, R. A.** 1955. The natural classification of the families of Coleoptera. Nathaniel Lloyd, London. 187 p.
- Evans, M. E. G.** 1961. The muscular and reproductive systems of *Atomaria ruficornis* (Marsham) (Coleoptera, Cryptophagidae). Trans. Roy. Soc. Edinb. 64:297-399.
- Gilbert, E. E.** 1952. The homologies of the male genitalia of Rhynchophora and allied Coleoptera. Ann. Ent. Soc. Amer. 45(4):633-637.
- Gurney, A. B., J. P. Kramer, and G. C. Steyskal.** 1964. Some techniques for the preparation, study and storage in microvials of insect genitalia. Ann. Ent. Soc. Amer. 57(2):240-242.
- Hieke, F.** 1966. Vergleichende funktionelle Anatomie der Abdominal muskulatur einiger männlicher Coleoptern unter besonderer Berücksichtigung des Genitoanalkomplexes. Deutsch. Ent. Z. N. F. Bd. 13, Hft. I-III:1-168.
- Hoffmann, A.** 1945. Faune de France 44, Coléoptères Bruchides et Anthribides. Lechavalier, Paris. 184 p.
- Iablokoff-Khuzorian, S. M.** 1966. Considerations sur l'édéage des Chrysomelidae et son importance phylogénique. l'Entomologiste 22(6):115-137.
- Johnson, C. D.** 1963. A taxonomic revision of the genus *Stator* (Coleoptera: Bruchidae). Ann. Ent. Soc. Amer. 56(6):860-865.
- Kingsolver, J. M.** 1962. A note on techniques. Ent. News 73:251.
- . 1964. The genus *Neltumius* (Coleoptera: Bruchidae). Coleop. Bull. 18(4):105-111.
- Lindroth, C. H.** 1957. The principal terms used for male and female genitalia in Coleoptera. Opusc. Ent. 22:241-256.
- Muir, F.** 1919. On the mechanism of the male genital tube in Coleoptera. Trans. Ent. Soc. London 1919:404-414, pl. 21.
- Mukerji, D., and M. A. H. Bhuya.** 1937. Reproductive system of the bruchid beetles, *Bruchus quadrimaculatus* Fabr. and *Bruchus chinensis* L. (Bruchidae-Coleoptera). Jour. Morph. 61(1):175-214.
- , and **S. N. Chatterjee.** 1951. Morphology of the genital structures of some of the Bruchidae (Lariidae) of India and Ceylon and their taxonomic importance. Indian Jour. Ent. 13(1):1-28.
- Powell, E. F.** 1941. Relationships within the family Chrysomelidae (Coleoptera) as indicated by the male genitalia of certain species. Amer. Midl. Nat. 25:148-195.
- Pu, C.** 1938. A comparative study of the musculature of the male genitalia in several species of Coleoptera. Lingnan Science Jour. 17:21-31.
- Sharp, D., and F. Muir.** 1912. The comparative anatomy of the male genital tube in Coleoptera. Trans. Roy. Ent. Soc. London. 1912(Pt. III):477-642.
- Snodgrass, R. E.** 1935. Principles of insect morphology. McGraw-Hill, New York. 667 p.
- . 1957. A revised interpretation of the external reproductive organs of male insects. Smiths. Misc. Coll. 135(6):1-60.
- Southgate, B. J.** 1958. Systematic notes on species of *Callosobruchus* of economic importance. Bull. Ent. Res. 49(3):591-599.
- , **R. W. Howe, and G. A. Brett.** 1957. The specific status of *Callosobruchus maculatus* (F.) and *Callosobruchus analis* (F.). Bull. Ent. Res. 48(1):78-89.

- Spilman, T. J.** 1952. The male genitalia of the Nearctic Salpingidae. *Coleop. Bull.* 6(1):9-12.
- Srivastava, U. S.** 1953. Reproductive organs of certain stored-grain beetles. II. Male organs of *Sitophylus oryzae*, *Laria affinis* and *Rhizopertha dominica*. *Proc. Nat. Acad. Sci., India* 23 (I-III):46-65.
- Verhoeff, C.** 1893. Vergleichende Untersuchungen über die Abdominalsegmente und die Copulationsorgane der männlichen Coleoptera, ein Beitrag zur Kenntniss der natürlichen Verwandtschaft derselben. *Deutsch. Ent. Z.* 1893, Hft. I: 113-170.
- Wilson, J. W.** 1930. The genitalia and wing venation of the Cucujidae and related families. *Ann. Ent. Soc. Amer.* 23(2):305-358.
- Wood, S. L.** 1952. Observations on the homologies of the copulatory apparatus in male Coleoptera. *Ann. Ent. Soc. Amer.* 45(4):613-617.
- Zacher, F.** 1930. Untersuchungen zur Morphologie und Biologie der Samen-käfer (Bruchidae-Lariidae). Beiträge zur Kenntnis der Vorratsschädlinge. 6. Beiträg. Arbeit. Biol. Reichanstlt. f. Land. u. Forst. Berlin, Bd. 18:233-384.
- Zia, Y.** 1936. Comparative studies of the male genital tube in Coleoptera Phytophaga. *Sinensia* 7(3):319-324, 326-327, 336-339.

THE GENUS OCHLEROPTERA IN NEW GUINEA

(HYMENOPTERA: SPHECIDAE)

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ABSTRACT—The discovery of a new species of Nyssoninae: Gorytini: *Ochleroptera novaguineensis* is the first record of the genus in New Guinea and in the Old World. It is hypothesized that the genus developed from a *Clitemnestra*-like ancestor and migrated from Australia north to New Guinea as well as east to South America.

Ochleroptera has previously been considered to be strictly a New World entity with 14 described species. *O. bipunctata* (Say) is the only United States representative of this gorytine wasp. *Ochleroptera* is petiolate and therefore a specialized offshoot of *Clitemnestra*, whose species occur in Australia and Chile. Dr. Karl Krombein of the United States National Museum has called my attention to a new species of *Ochleroptera* from northeastern New Guinea, sent to him from the Bishop Museum, Honolulu, Hawaii. This find greatly extends the range of *Ochleroptera* and leads me to believe that the genus developed in Australia, migrated north to New Guinea and, along with *Clitemnestra*, found its way along a different route east to the western shore of South America. From there it dispersed over much of the New World with one species reaching north of the Mexican border.